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THE MENDELIAN RATIO AND BLENDED INHERITANCE[1]

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THE indefatigable efforts of neo-Mendelists have succeeded in bringing numerous cases of inheritance, which had previously been considered incompatible with Mendel's law, into their domain by widening the original limitations. We still have many instances such as blended inheritance which can not apparently be harmonized with the law of Mendel. Recent experiments which demonstrate the existence of various degrees of dominance as well as the mutability of the determinants in their behavior, suggested to the writer that various forms of inheritance might be considered as degrees of modification of the law of Mendel. With this view in mind, I have attempted to obtain some general expression for the underlying principle of the law of inheritance by which means Mendel's original law may possibly be theoretically connected with the other cases. In fact, I was compelled to pursue this investigation in connection with my own experiments on the inheritance of the weight of the central nervous system, though this is not yet ready to present at this time.

In carrying out this investigation, I have assumed that the germ plasm is composed of many factors, the true nature of which is unknown, but which in one way or another determine the characters in the offspring. It is these hypothetical factors which are here provisionally called determinants. With this understanding, we may now proceed to the argument.

Suppose a gamete of one parent after the reducing division contains n determinants, the whole group of

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determinants being designated p, and the gamete of another parent also contains after the reducing division n determinants, the whole group being designated q. Then in the first hybrid zygote (F_1) there will be contained at the time of the union of the gametes $2n$ determinants. As we know, rearrangement takes place during the maturation of the germ cells and we assume this rearrangement to involve a random sampling by which n determinants are taken from the group of $2n$. From the theory of probabilities we find that n, $n-1$, $n-2$ . . . determinants of either parent contained in the gametes of F_1 are proportional to the successive terms of the following series:

$$p^n + np^{n-1}q + \frac{n(n-1)}{1\cdot 2}p^{n-2}q^2 + \frac{n(n-1)(n-2)}{1\cdot 2\cdot 3}p^{n-3}q^3 + \cdots. \quad (1)$$

The same phenomenon happens in the gametes of the other hybrid parent (F_1) and since the gametic constitution of the two hybrid parents is assumed to be identical with respect to the distribution of determinants (1), the frequency of the various combinations of the determinants in the second hybrid offspring (F_2) will be given by the square of (1) or

$$\left(p^n + np^{n-1}q + \frac{n(n-1)}{1\cdot 2}p^{n-2}q^2 + \frac{n(n-1)(n-2)}{1\cdot 2\cdot 3}p^{n-3}q^3 + \cdots\right)^2 \quad (2)$$

which may also be written as follows:

$$(p^2 + 2pq + q^2)^n.$$

This series, or the square of the binomial series, is then the most general expression for the gametic composition of any hybrid arising from a combination of p and q determinants and may therefore be considered as the underlying principle of any law of inheritance where the idea of determinants is used.

It is evident that since the somatic characters in question depend entirely on the behavior of the determinants, the relative frequency of various zygotes, as well as the character of the zygotes, depends on whether p or q de-

terminants are related as dominant and recessive, respectively, or whether they blend.

Suppose p is recessive and q is dominant in the Mendelian sense, we at once obtain from (2) the general expression for the alternative inheritance or

$$(RR + 2DR + DD)^n$$

where n refers to the number of allelomorphic pairs of characters, and the expansion gives a strict Mendelian ratio for any number of allelomorphic pairs of characters.

On the other hand, if we consider that p and q determinants blend with an equal intensity the series (2) will give all grades of hybrid characters between the two parental types, the frequency of which is proportional to the successive terms of a symmetrical point binomial curve, and the maximum frequency will be associated with the midparental types (case of equipotency). Castle's ('09) experiments with the length of the ear of rabbits illustrates this case.

Again let us suppose that p and q determinants blend, but with unequal intensity. According as p or q is prepotent, the zygote will resemble more closely one or the other parent. The frequency of each type of zygote again will be represented by the symmetrical point binomial curve. Thus the present series (2) represents both alternative and blended inheritance according to the behavior of the determinants.

The fact just mentioned, that the expressions for both blended and alternative inheritance are obtained from the same series which represent the gametic composition, suggests that we may possibly obtain cases of blending in character which normally follow the law of the alternative inheritance, and vice versa, and further we may even obtain both blended and alternative inheritance in the same offspring by subjecting the hybrid parents to different conditions, provided by such treatment we can modify the behaviors or functional activity of the de-

terminants, since as soon as the behavior is altered, we at once obtain from the series (2) another type of inheritance.

Although we have no clear direct evidence which demonstrates an occurrence of such extreme modification in the behavior of determinants, nevertheless the possibility of such an event is amply suggested by the recent experiments. For instance Tower ('10) has shown not only a reversal of dominance and apparent failure of segregation by merely modifying the environment of the beetles, but also a case in which the same parents produce offspring, some of which follow the law of Mendel while others show entirely different behavior with respect to dominance and segregation. Tennent ('10) was able to obtain from a cross of *Hipponoë esculenta* with *Taxopneustes variegatus,* reversal of dominance by decreasing the alkalinity of the sea water. Numerous samples of this sort can easily be found in the recent literature.

Whatever be the real condition or conditions which control the behavior of the determinants, one point is clear from the above, that the determinants are not immutable in their behavior, but subject to modification. This fact naturally leads us to think that we may obtain various forms of inheritance which are more or less different from the type form according to degree of functional modification. When a modification is maximum, we may even obtain a case of blended inheritance in a character which normally follows the law of alternative inheritance, or vice versa.

The facts mentioned above then indicate that our deduction from the properties of the formula is not at all improbable.

Again the properties of the formula suggests that we can theoretically connect cases of blended inheritance with those of alternative inheritance by the mere assumption that p or q fails to dominate either completely or incompletely. Since as we have shown by the degree

of dominance, the formula reduces to either equipotent or prepotent blending inheritance. From this standpoint we may consider that blending inheritance is a limiting case of alternative inheritance where either dominance is absent (equipotency) or is imperfect (heteropotency). If this hypothesis is accepted, then Mendel's law of alternative inheritance may be taken as the standard, and all cases referred to it or blending inheritance (though by this some more important features of inheritance are not suggested) may similarly be made the standard, the Mendelian ratios then becoming a special case.

In this connection Professor Davenport's ('07) view on the law of potency is of great interest. As his view of potency is so important, and especially as it clearly explains the relation between Mendelism and cases considered to be non-Mendelian, I shall quote his words at some length.

After quoting various cases of inheritance, Professor Davenport says:

> Taking all cases into account, it is clear that Mendel's law does not cover all; and if not, it must be a special case of a more inclusive law. Can we find a more general expression for the inheritance of characteristics which will cover all these cases? I think we can and that it may be called the law of potency. At the one extreme of the series we have equipotent unit characters, so that when they are crossed, the offspring show a blend, or a mosaic between them. At the other extreme is allelopotency. One of the two characteristics is completely recessive to the other. Between the two extremes of equipotency and allelopotency lies the great mass of heritable characteristics which when opposed in heredity, exhibit varying degrees of potency. This sort of inheritance may be called heteropotency.

Thus Professor Davenport shows also that Mendelian dominance is a particular case of potency, allelopotency, though he did not state that blending inheritance is a limiting case of Mendelism.

Whether a new expression "the law of potency" should be introduced as Professor Davenport has suggested, or whether the various potencies may be consid-

ered as a limiting case of Mendel's law of alternative inheritance, thus saving the original name, is a matter for later decision, though the latter name seems to me more appropriate to retain owing to the fact that the phenomenon of segregation, most important of all, had been first stated by Mendel.

Let us now consider a limiting case of our formula (2) when the values of n (number of allelomorphic pairs of characters) increase. In the typical Mendelian ratio, the relative frequency of the various zygotes with respect to any given visible character is proportional to an expansion of $(1+3)^n$ which is the same as $(1/4+3/4)^n$ if we consider the relative values of the frequencies. Thus in all known cases of the inheritance, we have to deal with an expansion of $(r+s)^n$ where $r+s=1$. A concise mathematical formula which represents a limiting case of the binomial series arising from an expansion of $(r+s)^n$ will be very useful, especially when we are dealing with a quantitative measurement such as weight, length, area, volume, etc., since in these cases the values of the variates will be graded. Further, the theoretical frequency corresponding to each variate when the value of n becomes very large, can best be determined from such a mathematical expression which represents a limiting case.

Without going into any detail of the mathematical treatment, it will be seen that we obtain two forms of expression according as $r=s$ or $r \neq s$. The former will be represented by the normal probability curve and the latter by a limiting case of a skew binomial curve. For representing a skew binomial curve we can best use DeForest's formula (Professor Pearson's curve of type 3). It may be useful to the reader to know that DeForest's formula degenerates into the normal probability curve as its simplest form, as will be seen below.

DeForest's formula (Hatai: '10) is usually written in the following form:

$$y = \frac{1}{k\sqrt{2\pi b}}\left(1 + \frac{x}{ab}\right)^{a^2b-1} e^{-ax},$$

where

$$k = 1 + \frac{1}{12a^2b} + \frac{1}{288(a^2b)^2} + \cdots.$$

$a =$ quotient of twice the second moment divided by the third moment.

$b =$ second moment.

Writing c for

$$\frac{1}{k\sqrt{2\pi b}}$$

we have

$$\log\left(\frac{y}{c}\right) = (a^2b - 1)\log\left(1 + \frac{x}{ab}\right) - ax$$

$$= (a^2b - 1)\left\{\frac{x}{ab} - \frac{1}{2}\left(\frac{x}{ab}\right)^2 + \frac{1}{3}\left(\frac{x}{ab}\right)^3 - \frac{1}{4}\left(\frac{x}{ab}\right)^4 + \cdots\right\} - ax$$

$$= -\frac{x^2}{2b} + \left(\frac{x^2}{3b} - 1\right)\frac{x}{ab} - \left(\frac{x^2}{4b} - \frac{1}{2}\right)\left(\frac{x}{ab}\right)^2 + \left(\frac{x^2}{5b} - \frac{1}{3}\right)\left(\frac{x}{ab}\right)^3 - \cdots.$$

Since for a vanishingly small value of the third moment, ab will be a very large number, consequently x/ab will be infinitesimal. Thus neglecting all terms in which x/ab is factor, we have

$$y = ce^{-\frac{x^2}{2b}}.$$

Restoring the value of C and remembering that for large values of ab, k reduces to unity, we finally have

$$y = \frac{1}{\sqrt{2\pi b}} e^{-\frac{x^2}{2b}}$$

which is the familiar formula for the normal probability curve.

From the above it is clear that DeForest's formula and its limiting case represent the frequency distribution of the zygotes, whether we are dealing with alternative or

blended inheritance. One, however, must not be misled to conclude that continuous variation necessarily means failure of segregation, since on the contrary apparent continuity may be a resultant of combinations of various segregating characters. Whether or not given data indicate a segregation, may be variously tested by some other means according to the nature of the experiment.

From the above we draw the following conclusions:

1. The series obtained from the square of the binomial expresses the distribution of determinants for both alternative and blended inheritance.

2. Blended inheritance may be considered to be a limiting case of alternative inheritance where dominance is imperfect. Thus Mendel's law of alternative inheritance may be considered as the standard and all other cases referred to it.

3. DeForest's formula with its limiting case adequately represents frequencies of all known cases of inheritance when the number of allelomorphic pairs of characters is large, especially when quantitative measurements are considered.

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